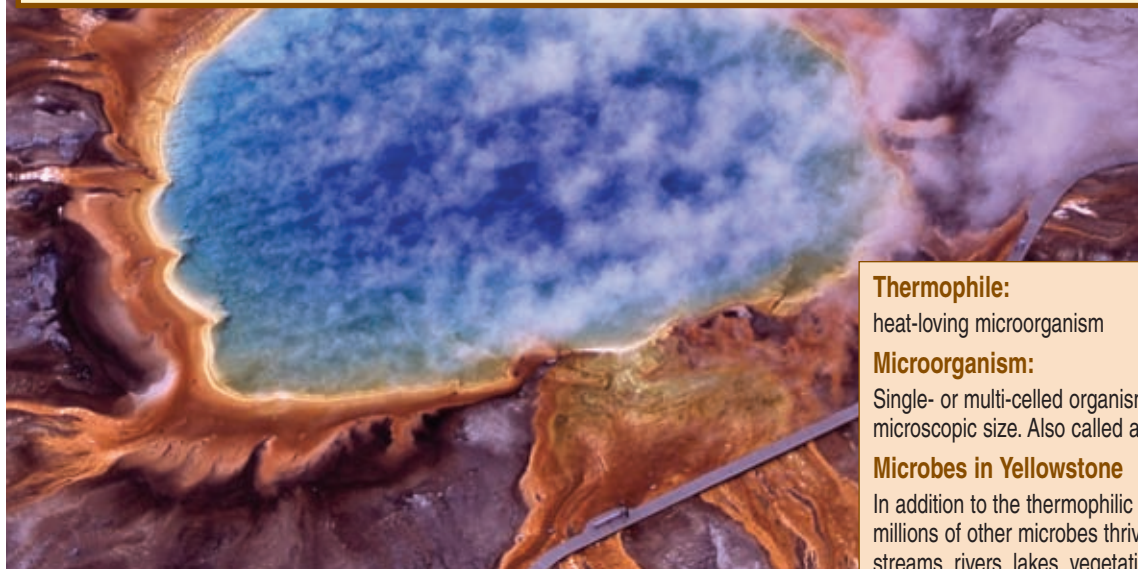


LIFE IN EXTREME HEAT

4



The hydrothermal features of Yellowstone are magnificent evidence of Earth's volcanic activity. Amazingly, they are also habitats in which microscopic organisms called thermophiles—"thermo" for heat, "phile" for lover—survive and thrive.

Grand Prismatic Spring at Midway Geyser Basin (above) is an outstanding example of this dual characteristic. Visitors marvel at its size and brilliant colors. Along the boardwalk (lower right of photo), they cross a vast habitat for thermophiles. Nourished by energy and chemical building blocks available in the hot springs, microbes construct vividly colored communities throughout the park. Living with these microscopic life forms are larger examples of life in extreme environments, such as mites, flies, spiders, and plants.

People for thousands of years likely have wondered about these extreme habitats. The color of Yellowstone's superheated environments certainly caused geologist Walter Harvey Weed to pause and think, and even question scientists who preceded him. In 1889, he wrote:

There is good reason to believe that the existence of algae of other colors, particularly the pink, yellow and red forms so common in the Yellowstone waters, have been overlooked or mistaken for deposits of purely mineral matter.

However, he could not have imagined what a fantastic world truly exists in these waters of brimstone. Species, unseen to the human eye, thrive in waters as acidic as the liquid in your car battery and hot enough to blister your skin. Some create layers that look like molten wax on the surface of calcium-rich steaming pools. Still others, apparent to us through the odors they create, exist only in murky, sulfuric caldrons that stink worse than rotten eggs.

Today, many scientists study Yellowstone's thermophiles. Some of these microbes are similar to the first life forms capable of photosynthesis—using sunlight to convert water and carbon dioxide to oxygen, sugars, and other byproducts. These life forms, called cyanobacteria, began to create an atmosphere that would eventually support human life. Cyanobacteria are found in some of the colorful mats and streamers of Yellowstone's hot springs.

Thermophile:

heat-loving microorganism

Microorganism:

Single- or multi-celled organism of microscopic or sub-microscopic size. Also called a microbe.

Microbes in Yellowstone

In addition to the thermophilic microorganisms, millions of other microbes thrive in Yellowstone's soils, streams, rivers, lakes, vegetation, and animals. Some of them are discussed in other chapters of this book.

Bacteria (Bacterium)

Single-celled microorganisms without nuclei, varying in shape, metabolism, and ability to move.

Archaea (Archaeum)

Single-celled microorganisms without nuclei and with membranes different from all other organisms. Once thought to be bacteria.

Viruses

Non-living parasitic microorganisms consisting of a piece of DNA or RNA coated by protein.

Eukarya (Eukaryote)

Single- or multi-celled organisms whose cells contain a distinct membrane-bound nucleus.

Other life forms—the archaea (see page 54)—predated cyanobacteria and other photosynthesizers. Archaea can live in the hottest, most acidic conditions in Yellowstone; their relatives are considered among the very earliest of life forms on Earth.

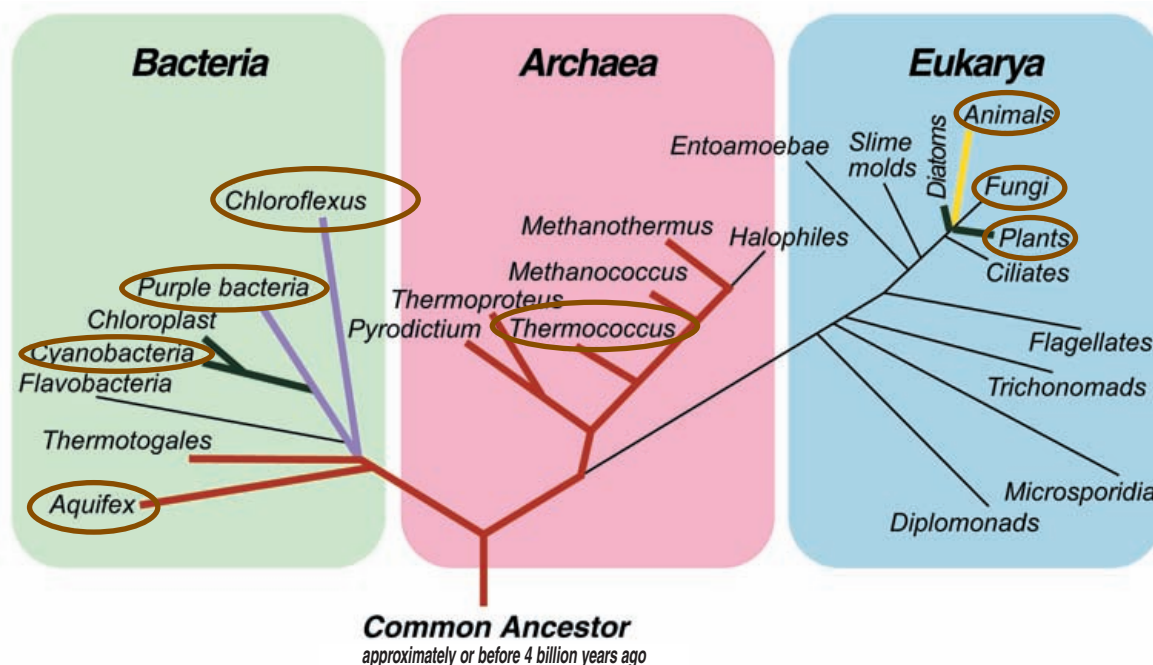
Yellowstone's thermophiles and their environments provide a living laboratory for scientists, who continue to explore these extraordinary organisms and how they relate to their environment. They know many mysteries of Yellowstone's extreme environments remain to be revealed.

Regardless of scientific advances, visitors and explorers in Yellowstone can still relate to something else Mr. Weed said about Yellowstone, more than a century ago:

The vegetation of the acid waters is seldom a conspicuous feature of the springs. But in the alkaline waters that characterize the geyser basins, and in the carbonated, calcareous waters of the Mammoth Hot Springs, the case is otherwise, and the red and yellow tinges of the algae combine with the weird whiteness of the sinter and the varied blue and green of the hot water to form a scene that is, without doubt, one of the most beautiful as well as one of the strangest sights in the world.

Thermophiles In the Tree of Life

In the last few decades, microbial research has led to a revised tree of life, far different from the one taught before. The new tree combines animal, plant, and fungi in one branch. The other two branches consist solely of microorganisms, including an entire branch of microorganisms not known until the 1970s—Archaea.



Yellowstone's hot springs contain species from the groups circled on the Tree of Life

Dr. Jack Farmer produced this image of the tree of life, which first appeared in GSA Today, July 2000. Used with permission.

Dr. Carl Woese first proposed this "tree" in the 1970s. He also proposed the new branch, Archaea, which includes many microorganisms formerly considered bacteria. The red line links the earliest organisms that evolved from a common ancestor. These are all hyperthermophiles, which thrive in water above 176°F (80°C), indicating life may have arisen in hot environments on the young Earth.

Relevance to Yellowstone

Among the earliest organisms to evolve on Earth were microorganisms whose descendants are found today in extreme high-temperature, and in some cases acidic, environments, such as those in Yellowstone. Their history exhibits principles of ecology and ways in which geologic processes might have influenced biological evolution.

Thermophilic Bacteria



Bacteria (bacterium)




single-celled microorganisms varying in shape, metabolism, and motility

The word “bacteria” is often associated with disease, but really only a few kinds of bacteria cause problems for humans. The other thousands of bacteria types, although all simple organisms, play a complex role in Earth’s ecosystems. In fact, cyanobacteria made our oxygen-rich atmosphere possible. They were the first photosynthesizers, more than 3 billion years ago. Without bacteria, we would not be here.

Almost any hot spring or geyser you see hosts bacteria. Some chemosynthesize, changing hydrogen or sulfur into forms other thermophiles can use. Most photosynthesize, providing oxygen to other thermophiles. All of

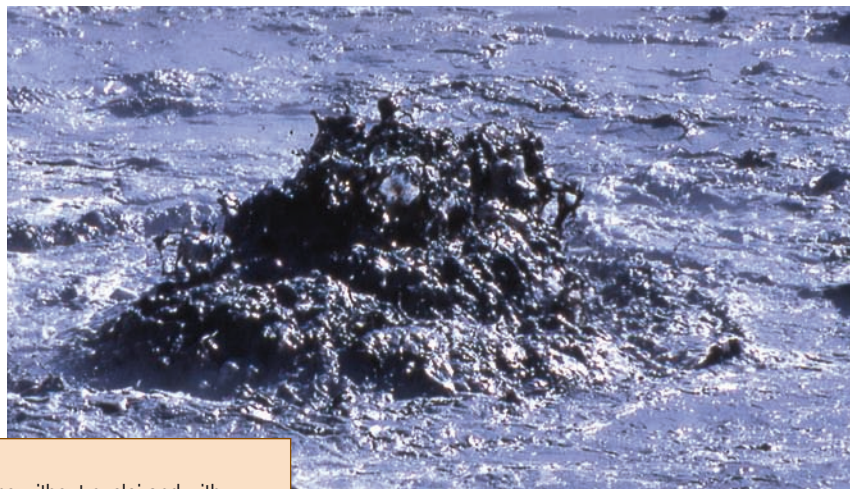
the cyanobacteria and green nonsulfur bacteria photosynthesize. Some fulfill both roles. For example, *Thermus sp.*—which are photosynthetic—also may be able to oxidize arsenic into a less toxic form.

Individual bacteria may be rod or sphere shaped, but they often join end to end to form long strands called filaments. These strands help hold thermophilic mats together, forming a vast community or mini-ecosystem. Other groups of bacteria form layered structures, which look like tiny towers, that can trap sand and other organic materials. (See bottom photo, page 58.)

	Name	pH & Temp	Description	Where found
	Cyanobacteria: <i>Calothrix</i> <i>Oscillatoria</i> <i>Phormidium</i> <i>Spirulina</i> <i>Synechococcus</i>	45–75°C 113–167°F usually alkaline	color: usually orange; can be yellow, blue-green, black metabolism: photosynthetic mobility: some can move to favorable light and temperatures within a mat form: usually long filaments entwined into mats with other thermophiles	Mammoth Hot Springs Upper, Midway, and Lower geyser basins West Thumb
	Green nonsulfur bacteria: <i>Aquifex</i> <i>Chloroflexus</i> <i>Thermus</i>	60–80°C 140–176°F usually alkaline	color: carotenoid pigments cause them to vary in pinks, yellows, and oranges metabolism: photosynthetic form: usually long filaments that entwine into mats with other thermophiles	Mammoth Hot Springs Upper, Midway, and Lower geyser basins West Thumb <i>Thermus sp.</i> at Norris, especially at Cistern Spring
	Sulfur-oxidizing bacteria: <i>Aquificales sp.</i>	60–86°C optimum >70°C	color: black, pink, or gray green, yellow, white metabolism: chemosynthesis, using hydrogen or sulfur form: filaments and mats	Lower Geyser Basin Mammoth Hot Springs: Angel Terrace

4

Thermophilic Archaea



Archaea (Archaeum)

single-celled microorganisms without nuclei and with membranes different from all other organisms. Once thought to be bacteria.

Archaea are the most extreme of all extremophiles—some kinds live in the frigid environments of Antarctica, others live in the boiling acidic springs of Yellowstone. These single-celled organisms have no nucleus, but have a unique, tough outer cell wall. This tough wall contains molecules and enzymes that may keep acid out of the organism, allowing it to live in environments of pH 3 or less. (Vinegar, for example, has a pH of less than 3.) Archaea also have protective enzymes within their cells.

Some scientists think present-day archaea have not changed much from their ancestors. This may be due to the extreme environments in which they live, which would allow little chance for successful changes to occur. If this is so, modern archaea may not be much different from the original forms—and thus provide an important link with Earth's earliest life forms.

Once thought to be bacteria, organisms in the domain Archaea actually may be more closely related to Eukarya—which includes plants

and animals.

Many kinds of archaea live in the hydrothermal waters of Yellowstone. For example, Grand Prismatic Spring at Midway Geyser Basin contains archaea. They are most well known in the superheated acidic features of Norris Geyser Basin and in the muddy roiling springs of the Mud Volcano area.

Whenever you see a hot, muddy, acidic spring, you are probably seeing the results of a thriving community of archaea called *Sulfolobus*. This is the archaea most often isolated and most well known by scientists. In sulfuric hydrothermal areas, it oxidizes hydrogen sulfide into sulfuric acid, which helps dissolve the rocks into mud. The *Sulfolobus* community in Congress Pool (Norris) is providing interesting new research directions for scientists: It is parasitized by viruses never before known on Earth. (See page 55.)

Name	pH & Temp	Description	Where found
Domain Archaea	pH: 0.9–5.8 upper temp.: >80°C/176°F	color: none metabolism: chemosynthesis, using hydrogen, sulfur, carbon dioxide form: unicellular, tough cell membrane	in many of Yellowstone's hydrothermal features
<i>Sulfolobus acidocaldarium</i> is the species most often isolated	pH 2–3, ideal <90°C/194°F	color: none metabolism: chemosynthesis; oxidizes sulfur and sulfur compounds into sulfuric acid form: spherical with lobes	Mud Volcano Norris, especially Congress Pool Roaring Mountain

Thermophilic Viruses



Viruses

non-living parasitic microorganisms consisting of a piece of DNA or RNA coated by protein

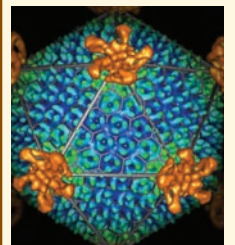
Like “bacteria,” the word “virus” often conjures up images of sickness and death. However, relatively few of the many types of viruses cause problems for humans. None of the thermophilic viruses in Yellowstone should cause problems for human health—our bodies are too cold, for one thing.

Unlike microorganisms in the three domains, viruses are not considered to be alive. They have no cell structure, only a protein “envelope” that encloses a piece of genetic material. They cannot reproduce on their own. Instead, a virus inserts itself into a host cell and uses that cell’s nutrients and metabolism to produce more viruses.

Scientists suspect many viruses exist in Yellowstone’s hydrothermal features because they would be a logical part of the thermophilic ecosystem. One kind was discovered in Congress Pool, at Norris Geyser Basin. It was infecting the archaeum *Sulfolobus*. Another kind of virus has been identified in pools near Midway Geyser Basin.

Name	pH & Temp	Description	Where found
Viruses (not in a domain)	pH: 0.9–5.8; optimum 2–3 55–80°C/ 131–176°F optimum 70–75°C	protein coats a core of genetic material cannot reproduce by itself reproduces by using the host cell’s metabolism not considered living predators of other microbes	in many of Yellowstone’s hydrothermal features
unnamed	acidic boiling	shape very similar to viruses that infect bacteria and animals, which could mean this group of viruses existed early in the development of life on Earth	unnamed pool near Midway Geyser Basin
unnamed	acidic boiling	parasitizes the archaeum, <i>Sulfolobus</i>	Norris, Congress Pool

this virus parasitizes
Sulfolobus



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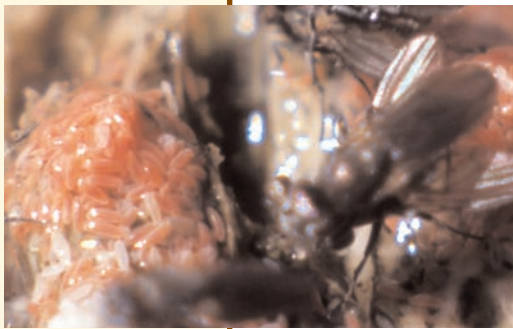
Thermophilic Eukarya

Eukarya (Eukaryote)

single- or multi-celled organisms whose cells contain a distinct membrane-bound nucleus



Zygogonium



ephydrid fly and egg mass



hot springs panic grass

Plants, animals, and mushrooms are the eukarya most of us know. Millions of unseen, microscopic members of this kingdom exist throughout our world, including in the extreme environments of Yellowstone.

Norris Geyser Basin (**photo above**) is one of the best places to see thermophilic algae. Bright green *Cyanidium caldarium* grows on top of orange-red iron deposits around Whirligig and Echinus geysers and their runoff channels. Waving streamers of *Zygogonium* are especially easy to see in Porcelain Basin, where their dark colors contrast with the white surface (**top photo at left**).

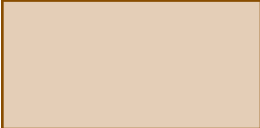


From the boardwalk crossing Porcelain Basin, you can also see larger eukarya, such as ephydrid flies. They live among the thermophilic mats and streamers, and eat, among other things, algae. The species that lives in the waters of Geyser Hill, in the Upper Geyser Basin, lays its eggs in pink-orange mounds, sometimes on the firm surfaces of the mats (**visible in center photo at left**). Part of the thermophilic food chain, ephydrid flies become prey for spiders, beetles, and birds.

Some microscopic eukarya consume other thermophiles. A predatory protozoan, called *Vorticella*, thrives in the warm, acidic waters of Obsidian Creek, which flows north toward Mammoth Hot Springs, where it consumes thermophilic bacteria.

Thermophilic eukarya include one form that is dangerous to humans: *Naegleria*, a type of amoeba, that can cause disease and death in humans if inhaled through the nose.

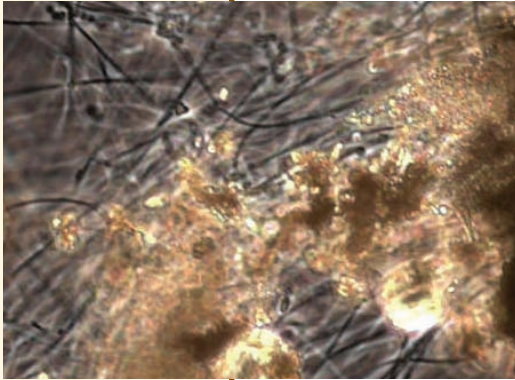
Although they aren't visible like mushrooms, several kinds of thermophilic fungi thrive in Yellowstone. *Curvularia protuberata* lives in the roots and leaves of hot springs panic grass (**bottom photo left**), which can grow on the edges of hot springs only with the aid of this fungus. The fungus contains the pigment melanin, which may somehow protect the plant from extreme heat. In return the fungus feeds on nutrients produced by the plant.

Of all the thousands (if not millions) of thermophilic species thriving in Yellowstone's extreme environments, the eukarya are the group that bridges the world of thermophilic microbes with the larger life forms—such as geese, elk, and bison—that thrive in ecological communities beyond the hot springs.

	Name	pH & Temp	Description	Where found
	Algae <i>Cyanidium caldarium</i>	pH 0.5–3 <56°C/133°F	color: bright green metabolism: photosynthetic form: coating on top of formations; mats	Roaring Mountain Norris, both basins
	<i>Zygonium</i>	35°C (95°F)	color: dark brown or purple metabolism: photosynthetic form: filaments and mats	Norris, especially Porcelain Basin
	Protozoa <i>Naegleria</i> (amoeba)	warm alkaline	predator; can infect humans when ingested through nose	Huckleberry Hot Springs Boiling River
	<i>Vorticella</i> (ciliate)		consumer; single-celled ciliate (feathery appendages swirl water, bringing prey)	Obsidian Creek
	Euglenids <i>Mutablis</i>	pH 1–2 <43°C/109°F	single-celled photosynthetic moves by waving one or two strands called flagella	
	Fungi <i>Curvularia protuberata</i>	<55°C/131°F	grows in roots and leaves of hot springs panic grass (<i>Dichanthelium lanuginosum</i>), enabling plant to survive high temperatures; in return the fungus feeds on sugars produced by the plant	
	Ephydrid fly <i>Ephydra</i> sp.	>pH 2 <43°C/109°F	nonbiting insect that eats microscopic algae as larvae and adult; prey for spiders, beetles, dragonflies, killdeer	Norris, especially Porcelain Basin Upper Geyser Basin, especially Geyser Hill
	Ross's bentgrass <i>Agrostis rossiae</i>	38°C/100°F	one of Yellowstone's two endemic plant species (see p. 66); may bloom in winter; dries out in summer's hot air temperatures	banks of Firehole River near Shoshone Lake
	Mostly warm springs spike rush, with some Tweedy's rush	warm acidic	forms thick floating mats, which also provide habitat for thermophilic algae and other thermophiles	Obsidian Creek

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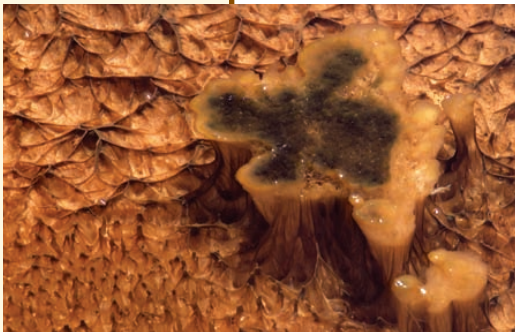
Thermophilic Communities



white filamentous bacteria, seen through a microscope



white filamentous bacteria



bacterial columns

Thermophilic communities are as diverse as the communities that humans live in. Community formations, colors, and locations vary depending on the types of microbes, the pH, and the temperature of their environments.

Millions of individual microbes can connect into long strands called filaments. Some bacteria (**photo left**) and algae form thin and delicate structures in fast moving water such as the runoff channels of hot springs and geysers. Other microbes form thick, sturdy structures in slower water or where chemical precipitates quickly coat their filaments.

A bacteria called *Thermocrinis* formed the structures in the **middle left photo**; this bacteria is descended from ancient bacteria that metabolized hydrogen and oxygen. Its filaments entwine, forming mats. Flowing water carries other microbes, miscellaneous organic matter, and minerals that become caught in the streamers and add to the mat.

Photosynthetic activity of cyanobacteria such as *Phormidium* form columns or pedestals (**bottom photo left**). Oxygen bubbles rise in the mat, forcing the microbes upward. The higher formations capture more organic matter and sediment than the lower mats, which help build the columns. Called stromatolites or microbialites, these structures are similar to ancient microbial communities still preserved in formations in some parts of the world.

Mats can be as thin as tissue paper or as thick as lasagna. Multiple layers of microorganisms comprise inch-thick mats. Dozens of types of microbes from all three domains can exist in these layers. Each microbial layer is a community, and each layer interacts with the other layers, forming a complex community full of millions of microorganisms and their life processes.

Visible and invisible changes occur in thermophile communities as light, temperature, and chemical concentrations change—both short term (within one day) and long term (seasonally). As day brightens to noon, cyanobacteria sensitive to light may move away from the surface; microbes less sensitive to light may move to the top layers of the mat. When light levels cause shifts in organisms, the community is responding to a *light gradient*.

Temperature and chemical gradients most often affect thermophilic communities in runoff channels of geysers and in shallow outflows from hot springs. In the **photo above**, the runoff channels from Pinwheel and Whirligig geysers meet. The outer edge of both are too hot for visible thermophile communities to develop. But as Pinwheel's water cools in the shallower channel edge, *Cyanidium* (an alga) can grow, forming a bright green community. Whirligig's runoff is hotter, which prevents *Cyanidium* from growing, but another type of



Chocolate Pots, on the Gibbon River, are an iron-rich community.

Thermophile community inhabitants are controlled, in part, by water temperature and pH. The chart at right provides general guidelines for what lives in which temperature.

thermophile thrives by oxidizing the abundant iron in the water, forming the orange community.

At the Chocolate Pots (**photo above**), which you can see from pullouts along the Gibbon River just north of Gibbon Meadows, iron-rich water flows from the vents. Three kinds of cyanobacteria—*Synechococcus*, *Chloroflexus*, and *Oscillatoria*—thrive in the iron-rich waters that flow from the vents. The bacterial filaments form mats, in which the mineral is captured. The iron may also be caught on the bacteria as the microbes move about within the mat. An olive green color indicates where the orange iron and green bacteria are enmeshed. Darker streaks indicate the presence of manganese. Scientists think the bacterial concentration may contribute to the iron concentrations at the Chocolate Pots, which are one hundred times more concentrated here than at other neutral hydrothermal features.

Communities formed by thermophilic microbes sustain communities of larger organisms within Yellowstone's hydrothermal areas, some of which were described on pages 56–57. These communities in turn affect even larger communities of the park's mammals. For example, bison and elk find food and warmth on the less extreme edges of thermophilic environments in winter (*photos at right*). In turn, coyotes, wolves, and bears seek prey in these areas—especially in late winter and early spring when bison and elk are weaker than any other time of year.

Whether it's the strike of a grizzly's paw or the shift of heat beneath the earth, these communities change through common and strange forces. Biologists continue to discover more about the individuals involved in thermophilic communities, and ecologists continue to follow the threads of these intricate webs.



93°C/199°F
Archaea

73°C/163°F
Cyanobacteria

62°C/144°F
Fungi

60°C/140°F
Algae

56°C/133°F
Protozoa

50°C/122°F
Mosses
crustaceans
insects

27°C/80°F
Trout

4

Thermophiles by Place & Color

Upper, Midway, & Lower Geyser Basins and West Thumb Geyser Basin



Characteristics

- pH 7–11
- underlain by rhyolitic rock
- water rich in silica, which forms sinter and geysers deposits

Thermophiles by Temperature

- >75°C/167°F, bacteria and archaea
- >75°C/167°F, *Thermocrinis* and other bacteria form streamers of pink, yellow, orange, or gray.
- <75°C/167°F, *Synechococcus*, *Phormidium*, and *Calothrix* (cyanobacteria) plus *Roseiflexus* (filamentous green bacterium) form mats that line cooler hot springs and runoff channels

Thermophiles by Color

- pink, yellow, orange, gray filaments—*Thermocrinis* bacteria
- orange mats—cyanobacteria, especially on sunny summer days (carotenoids protect the organisms from the bright sun)
- olive-green mats—cyanobacteria mixed with iron

Norris Geyser Basin & Mud Volcano Area



- pH 0–5
- underlain by rhyolite rock

- >75°C/167°F, *Sulfolobus*, an archaeum, and viruses that parasitize *Sulfolobus*
- >60°C/140°F, filamentous bacteria in yellowish streamers and mats
- <60°C/140°F, filamentous bacteria and archaea form red brown mats
- <56°C/133°F, *Zygonium*, other algae, and fungi form mats in runoff channels

- pink–pinkish-orange mats and streamers—*Thermus aquaticus* and other *Thermus* sp.
- green streamers and mats—*Cyanidium*
- orange—iron and/or arsenic, perhaps oxidized by thermophiles
- gray, muddy pools—*Sulfolobus*

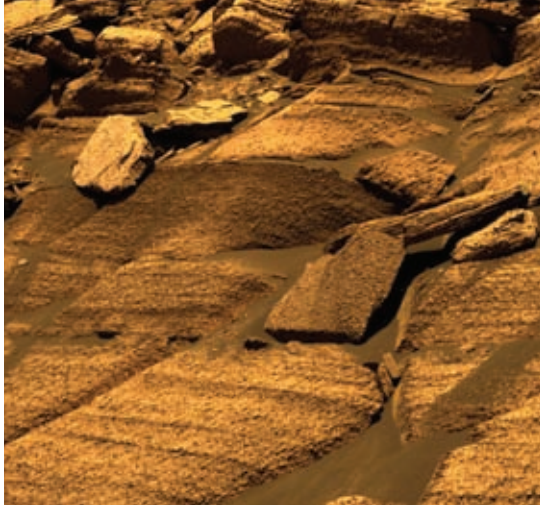
Mammoth Hot Springs



- pH 6–8 (neutral to slightly acidic)
- underlain by ancient limestone deposits
- water rich in calcium carbonate and sulfur

- 66–75°C/151–167°F, *Aquificales* (bacteria) filaments near hot springs vents
- <66°C/151°F, *Chloroflexus* (green nonsulfur bacteria) and cyanobacteria mats, and filamentous bacteria streamers
- <58°C/136°F, *Chromatium* (bacteria) form dark mats (uncommon)
- 25–54°C/77–129°F, *Chlorobium* (bacteria) mats; *Calothrix* streamers; *Synechococcus*

- Orange—*Chloroflexus* and cyanobacteria in summer
- Green—*Chloroflexus* and cyanobacteria in winter; *Chlorobium* in cooler water
- Cream—filamentous bacteria



These layers of rock on Mars have minerals and features developed by interactions between liquid water and rocks over extended periods of time. This evidence does not prove that life developed on Mars, but it brings the possibility one step closer to reality.
Photo and text adapted from www.nasa.gov, image by Nasa/JPL

From Earth to Mars—and Beyond?

Yellowstone's hydrothermal features and their associated communities of ther-

mophiles are studied by scientists who are searching for evidence of life on other planets. The connection is extreme environments. If life began in the extreme conditions thought to have been widespread on ancient Earth, it may well have developed on other planets—and might still exist today.

The chemosynthetic microbes that thrive in some of Yellowstone's hot springs do so by metabolizing inorganic chemicals, a source of energy that does not require sunlight. Such chemical energy sources provide the most likely habitable niches for life on Mars or on the moons of Jupiter—Ganymede, Europa, and Callisto—where uninhabitable surface conditions preclude photosynthesis. Chemical energy sources, along with extensive groundwater systems (such as on Mars) or oceans beneath icy crusts (such as on Jupiter's moons) could provide habitats for life.

Similar Signatures

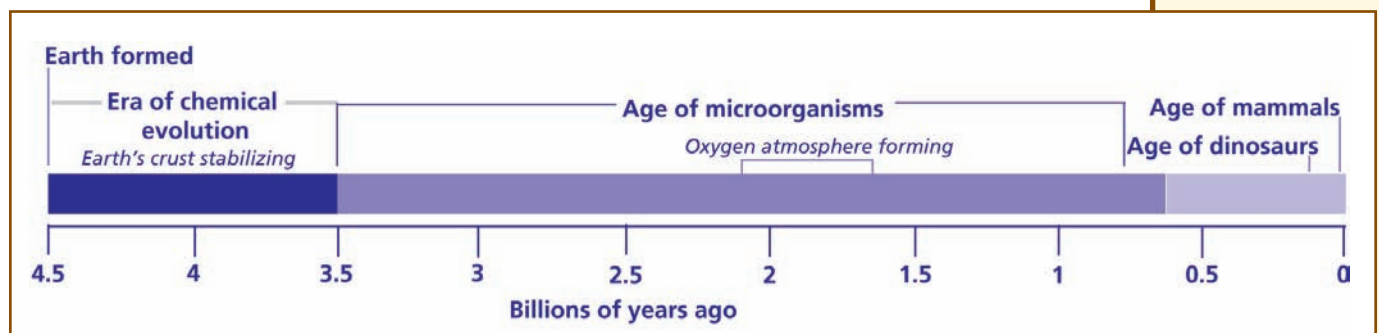
Thermophile communities leave behind evidence of their shapes as biological “signatures.” For example, at Mammoth Hot Springs, rapidly depositing minerals entomb thermophile communities. Scientists compare these modern signatures to those of ancient deposits elsewhere, such as sinter deposits in Australia that are 350 million years old. These comparisons help scientists better understand the environment and evolution on early Earth, and may give them an idea of what to look for on other planets.

Yellowstone National Park will continue to be an important site for studies at the physical and chemical limits of survival. These studies will give scientists a better understanding of the conditions that give rise to and support life, and how to recognize signatures of life in ancient rocks and on distant planets.

What's the Connection?

- Yellowstone's hydrothermal features contain modern examples of Earth's earliest life forms, both chemo- and photosynthetic, and thus provide a window into Earth's ancient past.
- Yellowstone hydrothermal communities reveal the extremes that life can endure, providing clues to environments that might harbor life on other worlds.
- Yellowstone environments show how mineralization preserves biosignatures of thermophilic communities, which could help scientists recognize similar signatures elsewhere.
- Based on the history of life on Earth, the search for life on other planets seems more likely to encounter evidence of microorganisms than of more complex life.

For additional information about the scientific value of thermophiles, see Chapter 9, “Bioprospecting.”



- Barns, Susan et al. 1996. Perspectives on archaeal diversity, thermophily, and monophyly from environmental rRNA sequences. *Proceedings Natl Acad. Sci.* 93: 9188–9193
- Boomer, Sarah et al. 2002. Molecular characterization of novel red green non-sulfur bacteria from five distinct hot spring communities in Yellowstone National Park. *Applied and Environmental Microbiology*. January: 346–355.
- Brock, Thomas D. 1978. *Thermophilic microorganisms and life at high temperatures*. Springer-Verlag, New York.
- 1998. Early days in Yellowstone Microbiology. *ASM News*. 64:137-140
- T. D. 1994 *Life at High Temperatures* Yellowstone Association/Mammoth, WY
- Dyer, Betsey Dexter 2003 *A Field Guide to Bacteria* Cornell University/Ithaca
- Carsten, Laura. 2001. Life in extreme environments. *Northwest Science and Technology*. Spring: 14–21.
- Farmer, Jack D. 2000. Hydrothermal Systems: Doorways to Early Biosphere Evolution. *GSA Today* 10(7): 1–9.
- Farmer, J. D., and D. J. Des Marais. 1999. Exploring for a record of ancient Martian life. *J. Geophys. Res.* 104.
- Fouke, Bruce et al. 2000. Depositional facies and aqueous-solid geochemistry of travertine-depositing hot springs. *J Sedimentary Research* 70(3): 565–585.
- Gihring, Thomas et al. 2001. Rapid arsenite oxidation by *T. aquaticus* and *T. thermophilus*: Field and laboratory investigations. *Environ. Sci. Technol.* 35:3857–3862.
- Madigan, Michael and Aharon Oren. 1999. Thermophilic and halophilic extremophiles. *Current Opinion in Microbiology* 2: 265–269.
- Pierson, Beverly and Mary Parenteau. 2000. Phototrophs in high iron microbial mats: microstructure of mats in iron-depositing hot springs. *Microbiology Ecology* 32: 181–196.
- Reysenbach, A-L. et al, eds. 2001. *Thermophiles: Biodiversity, Ecology, and Evolution*. Kluwer Academic Press/Plenum, New York.
- Reysenbach, A-L and Sherry Cady. 2001. Microbiology of ancient and modern hydrothermal systems. *Trends in Microbiology* 9(2): 80–86.
- Reysenbach, A-L, et al. 2000. Microbial diversity at 83°C in Calcite Springs, Yellowstone National Park. *Extremophiles* 4: 61–67.
- Sheehan, K.B. et al. 2005. *Seen and Unseen: Discovering the Microbes of Yellowstone* Falcon/Helena
- Sheehan, K.B. et al. 2004. *Yellowstone Under the Microscope*. The Globe Pequot Press/Gilford, CT.
- Walter, M. R. and D. J. Des Marais. 1993. Preservation of biological information in thermal spring deposits: developing a strategy for the search for fossil life on Mars. *Icarus* 101: 129–143.
- Ward, D.M. 1998. Microbiology in Yellowstone National Park. *ASM News* 64:141–146.
- Ward, D.M. et al. 1992. Modern phototrophic microbial mats: anoxygenic, intermittently oxygenic/anoxygenic, thermal, eucaryotic and terrestrial. In *The Proterozoic Biosphere: a Multidisciplinary Study*, J.W. Schopf and C. Klein, eds. Cambridge Univ. Press/Cambridge.
- Ward, D.M. and R.W. Castenholz. 2000. Cyanobacteria in geothermal habitats. In *Ecology of Cyanobacteria*. Kluwer Academic Publishers
- Ward, D.M. et al. 2002. Natural history of microorganisms inhabiting hot spring microbial mat communities: clues to the origin of microbial diversity and implications for micro- and macro-biology. In *Biodiversity of Microbial Life: Foundation of Earth's Biosphere*, J.T. Staley and A.-L. Reysenbach, eds. John Wiley and Sons/New York.

Websites

- www.windowsintowonderland.org, "Hot Colors: Windows into Hidden Worlds" (electronic field trip)
- www.microbeworld.org, the public website of the American Society for Microbiology
- www.tbi.montana.edu, website of the Thermal Biology Institute of Montana State University
- Additional information available on numerous websites. Search topics include thermophiles, extreme life, and astrobiology.

Additional Information from Yellowstone National Park

- Yellowstone National Park website, www.nps.gov/yell, includes an array of park information about resources, science, recreation, and issues.
- Yellowstone Science*, published quarterly, reports on research and includes articles on natural and cultural resources. Free; available from the Yellowstone Center for Resources, in the Yellowstone Research Library, or online at www.nps.gov/yell.
- Yellowstone Today*, published seasonally and distributed at entrance gates and visitor centers, includes features on park resources such as hydrothermal features.
- Area trail guides detail geology of major areas of the park. Available for a modest donation at Canyon, Fountain Paint Pot, Mammoth, Norris, Old Faithful, and West Thumb areas.
- Site Bulletins, published as needed, provide more detailed information on park topics. Free; available upon request from visitor centers.